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A review of *Tetramopria* (Hymenoptera, Diapriidae, Diapriinae) of the Eastern Palaearctic with notes on mating behaviour and interactions with host ants

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Abstract

Eastern Palaearctic *Tetramopria* are reviewed; the previously unknown female of *T. turbinata* is described; *T. tortilis* is newly recorded from Korea and *T. turbinata* is newly recorded from Japan; an updated key for all Palaearctic *Tetramopria* species is given. For both Eastern Palaearctic *Tetramopria* species we report observations of mating, and interactions between the wasps and their host ants.

Keywords

Behaviour, copulation, courtship, description, host-parasitoid interaction, key, myrmecophile

Introduction

Tetramopria Wasmann, 1899 is a genus from the Diapriini (Diapriinae, Diapriidae) with five undoubted species found in the Palaearctic region. (Pschorn-Walcher 1957; Johnson 1992; Notton 1994, 2004). The four species excluding *T. castanea* (Kieffer, 1911) were divided into two species-groups: the *aurocincta* and the *cincticollis* groups (Notton 1994). The two species-groups are distinguishable based on differences in the structure of the scutellar disc, anterior scutellar pit, anterior margin of T2, female

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antenna, male mid leg and male F1. *Tetramopria castanea* was transferred from the genus *Diapria* to *Tetramopria* by Notton (2004). It was also suggested that it was morphologically similar to *T. aurocincta* Wasmann, 1899 because it had a keeled scutellar disc. However, it was not then assigned to a species-group. Three further doubtful species have been reported from the Australian region: the absence of an anterior scutellar pit suggests these are wrongly classified (Dodd 1924). *Tetramopria* species show a number of features correlated with myrmecophile habits including reduced eye size and the yellowish collar of pronotal setae (Notton 1994). The European species *T. aurocincta* has been reared as a gregarious parasitoid from the puparia of tachinid flies parasitic on lepidopterans (Szelényi 1957; Masner in Jasič 1964) and both *T. aurocincta* and *T. cincticollis* Wasmann, 1899 have been recorded as symphiles in the nests of the ant *Tetramorium caespitum* (Linnaeus, 1758) (Wasmann 1899).

In the Eastern Palaearctic region, two species of *Tetramopria* have been described: *T. tortilis* Notton, 1994 based on female and male from Japan and *T. turbinata* Notton, 1994 based on a single male from Korea. *T. tortilis* was rediscovered in Japan by Kawai et al. (2024). Little was previously known about the biology of this genus although in Japan an unidentified species of *Tetramopria* was collected from the nests of *Tetramorium tsushimae* Emery, 1925 (Maruyama et al. 2013) and Kawai et al. (2024) proposed a probable association between *T. tortilis* and *Tetramorium tsushimae.* Recently RK found several Japanese *Tetramopria* specimens in museum collections and we can now describe the previously unknown female of *T. turbinata* and provide a more complete identification key to Palaearctic *Tetramopria* species. In addition, SY has discovered the genus *Tetramopria* during a field survey of ants in Korea and, by conducting captive observations, has been able to add greatly to our knowledge of courtship and copulation of these parasitoids and of their behavioural interactions with the host ants.

Material and methods

Materials examined are deposited in the collections of the following institutes: Entomological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka, Japan (ELKU); Nagoya Biodiversity Center, Nagoya, Japan (NBC) (the specimens in the Center were deposited at the Entomological Laboratory, Faculty of Agriculture, Meijo University, Nagoya, Japan (ELMU)). Museum material for this study was collected by Malaise trap (MT), yellow pan trap (YPT), and emergence trap (EmT). Morphological terminology and abbreviations follow Naumann (1982), Masner and García (2002), Yoder (2004) and Yoder et al. (2010). The term RSS is used after Isidoro et al (1996). The measurements mostly follow Masner and García (2002). Photos of dried specimens were taken using a Canon MP-E65 mm macro lens mounted on a Sony α7R IV digital camera or a Canon EOS M200 mounted on an Olympus SZX10 (for mesosoma in ventral view of *T. tortilis*, propodeum and anterior part of T2, and tip of metasoma of *T. turbinata*). Mid legs were mounted in Euparal on a cover slip glued onto a paper card and pinned under the respective specimen (Maruyama 2004). The

photos of mid legs were taken by a Canon EOS Kiss X8i camera attached to an Olympus BX50 microscope. Photos of living specimens were taken using a Nikon d7500 digital camera with Kenko macro lens, AF-S Micro NIKKOR 60mm f/2.8G ED and Godox MF12 strobes. Individual photos were stack-combined with Zerene Stacker (Zerene Systems LLC) and processed in Adobe Photoshop. SY collected adults of both *Tetramopria* species and their host ants between April and August 2024, at Ulsan city, Korea. SY maintained parasitoid and ant colonies for observation in polypropylene insect breeding jars (external diameter 100.00 mm, external height 40.00 mm, internal diameter: 91.35 mm, internal height 38.50 mm, ventilation hole 40.00 mm covered with mesh, manufactured by SPL Life Sciences) and provided with food (honey water and mosquitoes). Humidity of the jars was controlled by spreading a layer of hydrated gypsum plaster in the bottom of the jar and placing tissue on top of it.

Results

Tetramopria Wasmann, 1899

Tetramopria Wasmann, 1899: 127. Type species *Tetramopria aurocincta* Wasmann, 1899.

Diagnosis. Head in dorsal view hexagonal, tapered behind eyes, without projections or depressions (Figs 1F, 4F); antennal shelf prominent; eye small; setae of temple straight and directed downwards; occiput with a dense golden cushion of setae; female flagellum 10-segmented with 4- or 5-segmented expanded clava; F10 slightly narrower than F9; male flagellum 12-segmented, without long whorled setae, F2 modified. Pronotal collar with a narrow, dense, golden, cushion of setae (Figs 1C, 4B); notauli absent; scutellum with anterior scutellar pit; scutellar disc tectiform, with a sharp medial keel or flat to weakly raised, with short, blunt keel (Figs 1C, 4B, D). Fore wing without basal vein. Propodeum slightly concave posteromedially, without specialized flanges at sides. Tarsi cylindrical, with tarsomeres about as high as wide. Petiole in lateral view slightly raised, not elevated above level of anterior margin of T2; anterior margin of T2 entire, wider than width of petiole.

We have followed the interpretation of *Tetramopria* used by Notton (1994). This concept is very similar to that of Sundholm (1960) who provided a key to separate *Tetramopria* from *Diapria* Latreille, 1796, *Trichopria* Ashmead, 1893 and *Viennopria* Jansson, 1953, and the concept of Huggert and Masner (1983) who keyed *Tetramopria* from additional Holarctic genera of myrmecophile Diapriini not covered by Sundholm (1960).

Remarks. Based on the original description, *Tetramopria castanea* (Kieffer, 1911) satisfies the definition of the *aurocincta* group of Notton (1994); scutellar disc tectiform with a sharp medial keel; female antennal clava four-segmented. Therefore, although the states of the anterior scutellar pit and T2 are unknown, *T. castanea* is included in the *aurocincta* group.

Key to species of the Palaearctic *Tetramopria* (modified from Notton 1994)

1 Scutellar disc tectiform, with a sharp medial keel covering its entire length and into anterior scutellar pit (Fig. 4B); anterior scutellar pit smooth, rarely weakly striate to costate (Fig. 4B); T2 with two shallow foveae subbasally; female antennal club 4-segmented; male with mid-trochanter and mid-tibia unmodified (Fig. 4H) and with F1 less elongate, about 2.5 times as long as greatest width (*aurocincta* group) **2**

– Scutellar disc flat to weakly raised, with at most a short, blunt keel (Fig. 1C); anterior scutellar pit strongly costate from front to back (Fig. 1C); T2 without subbasal foveae; female antennal club 5-segmented; male with mid-trochanter expanded, triangular, with mid-tibia strongly twisted (Fig. 1H) and with third antennal segment more elongate, about 4.0 times as long as greatest width (*cincticollis* group)..... **4**

2 Anterior scutellar pit divided into two foveae..... ***T. castanea*** **(Kieffer, 1911)**

– Anterior scutellar pit single **3**

3 Scutellar disc not emarginate posteriorly; basal margin of large tergite slightly concave, without carinae, basal foveae smooth; dorsal propodeal areas less deeply foveate; frons less convex; antenna less robust; mesopleuron with more hairs in lower half ..... ***T. aurocincta*** **Wasmann, 1899**

– Scutellar disc broadly emarginate posteriorly; basal margin of large tergite undulate, with two oblique carinae, basal foveae striate; dorsal propodeal areas more deeply foveate; frons more convex; antenna more robust; mesopleuron with fewer hairs in lower half..... ***T. turbinata*** **Notton, 1994**

4 Male F1 without sub-apical tooth on inner side; scutellar disc flat and smooth; mesopleuron without pronounced ventral concavity in front of mid coxae ... . ***T. cincticollis*** **Wasmann, 1899**

– Male F1 with sub-apical tooth on inner side; scutellar disc domed, weakly tectiform and weakly striate or weakly rugose; mesopleuron with pronounced ventral concavity in front of mid coxae ..... ***T. tortilis*** **Notton, 1994**

Tetramopria tortilis **Notton, 1994**

Figs 1–3

Specimens examined. (2♂♂6♀♀) Japan • 1♀; Ibaraki Pref., Ishioka, Ishikawa; 11 IV 2024; Y. Komatsuzaki leg.; (ELKU) • 1♂1♀; Nagano Pref., Matsumoto, Jôyama; 5 IV 2010; T. Komatsu leg.; from nest of *Tetramorium tsushimae*; (ELKU) • 1♀; Shizuoka Pref., Iwata, River Ohta, YPT, 16 VI 2001, M. Urai leg. (NBC) • 1♀, Aichi Pref., Kasugai, Takagi, deciduous forest; EmT; 15–21 VI 1994; K. Sanda leg.; (NBC). South Korea • 2♀♀; Ulsan Metropolitan City, Ulju-gun, Cheongnyang-eup, Munjuk-ri; 24 VI 2024; Seonwoo Yoon leg.; from nest of *Tetramorium tsushimae*; (ELKU) • 1♂; Ulsan Metropolitan City, Ulju-gun, Cheongnyang-eup; Munjuk-ri; 1 VII 2024; Seonwoo Yoon leg.; from nest of *Tetramorium tsushimae*; (ELKU).

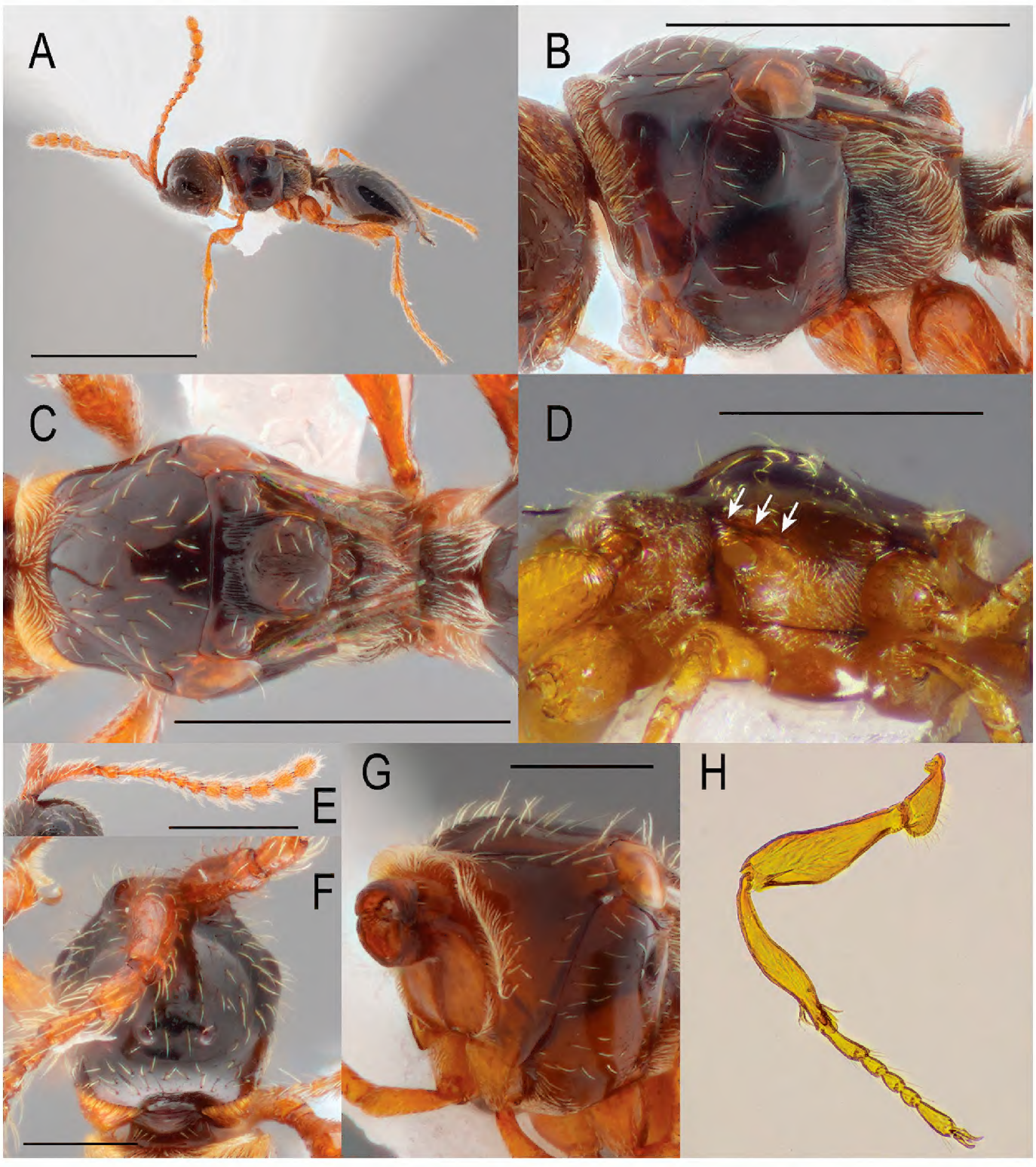

Figure 1. *Tetramopria tortilis* male from South Korea (**H**) and female (**A–G**) from Japan: **A** lateral habitus **B** mesosoma, lateral view **C** mesosoma, dorsal view **D** mesosoma, ventral view **E** antenna, lateral view **F** head, dorsal view **G** mesosoma, latero-ventral view **H** mid leg; *white arrows* postpectal carina. Scale bars: 1.0 mm (**A**); 0.5 mm (**B, C, E**); 0.3 mm (**D**); 0.2 mm(**F, G**).

Diagnosis. Female flagellum 10-segmented with 5-segmented gradually expanded clava; male F1 about 4.0 times as long as its greatest width. Propleuron smooth and shiny, with a small area of pubescence latero-ventrally (Fig. 1G). Anterior scutellar pit strongly costate (Fig. 1C); scutellar disc weakly raised, with a short, blunt keel medially (Fig. 1C). Mesopleuron with postpectal carina ventrally (Fig. 1D, white arrow) and broad mesocoxal depression, forming a pronounced ventral concavity in front of mid coxae in lateral view (Fig. 1B). Male with mid-trochanter expanded, triangular, with mid-tibia strongly twisted. T2 without subbasal foveae.

Variation. Body length 1.8–2.3 mm.

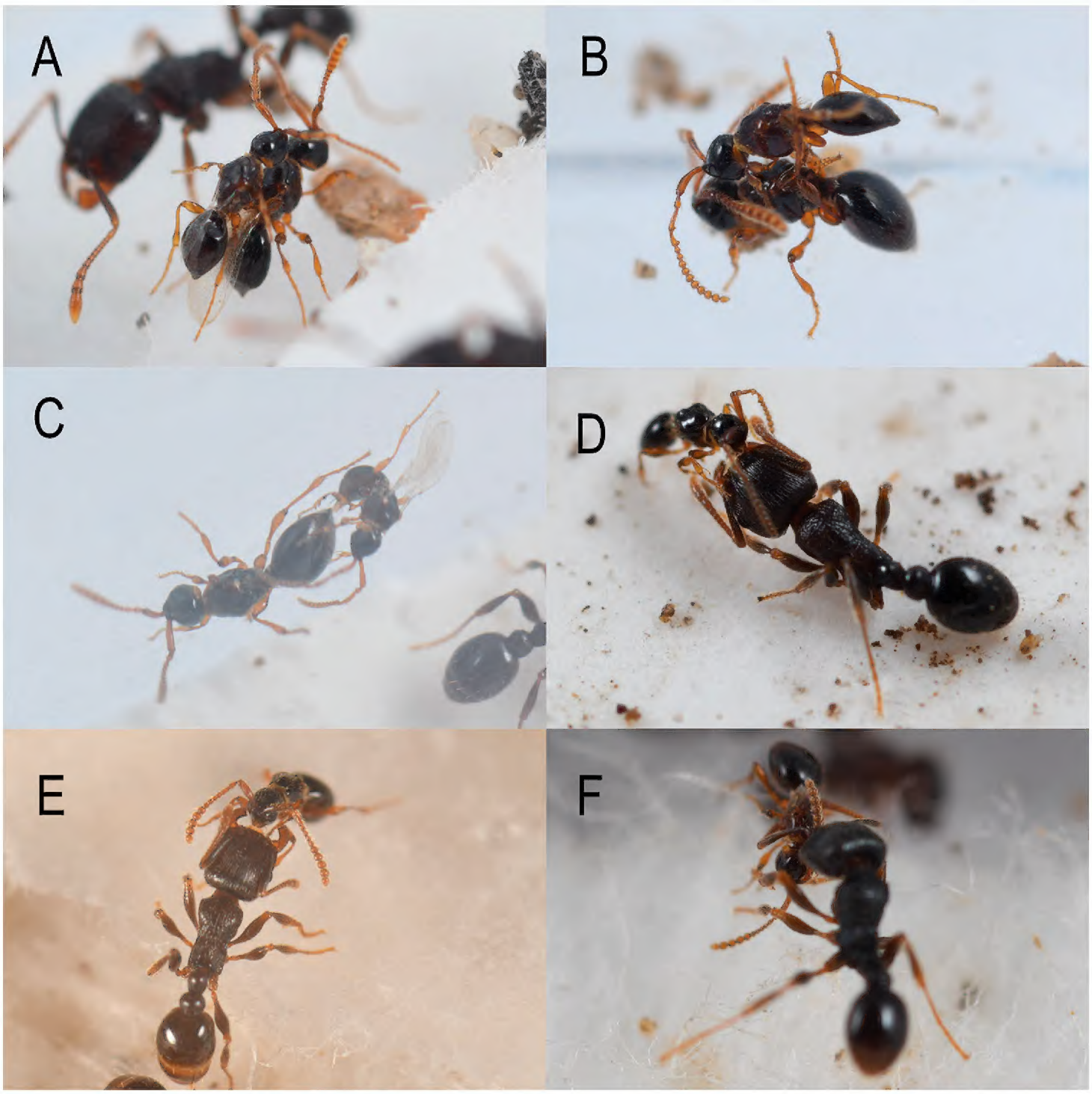

Figure 2. Courtship of *Tetramopria tortilis* (**A–C**) and interaction of *T. tortilis* and *Tetramorium tsushimae* (**D–F**): **A** male wasp mounted on a female holding the female's wings with his mid legs and with his fore-legs extended laterally and hind legs posteriorly **B** female wasp trying to push the male off with her hind legs **C** male wasp grasping female metasoma with his fore and middle legs, and with his hind legs remaining on the substrate **D** mouth to mouth contact between male wasp and worker ant **E** mouth to mouth contact between female wasp and worker ant **F** worker ant biting antenna of female wasp and carrying female wasp.

Distribution. Japan (Honshu: Ibaraki, Nagano, Shizuoka, Aichi; Kyushu?) (Notton 1994; Maruyama et al. 2013; Kawai et al. 2024). South Korea, new record. In Maruyama et al. (2013), Kyushu was also listed as a locality. However, this record was not based on specimens, but rather on observations by Dr. T. Komatsu (Dr. Maruyama per. comm.). As we were unable to confirm any specimens from Kyushu, this record needs confirmation.

Biology. *Tetramopria tortilis* has been collected from the nests of *Tetramorium tsushimae* Emery, 1925 both in Japan and Korea. In Ibaraki Prefecture (Japan) *Tetramopria tortilis* was collected from a nest of *Pristomyrmex punctatus* (Smith, 1860), but based on the ecological

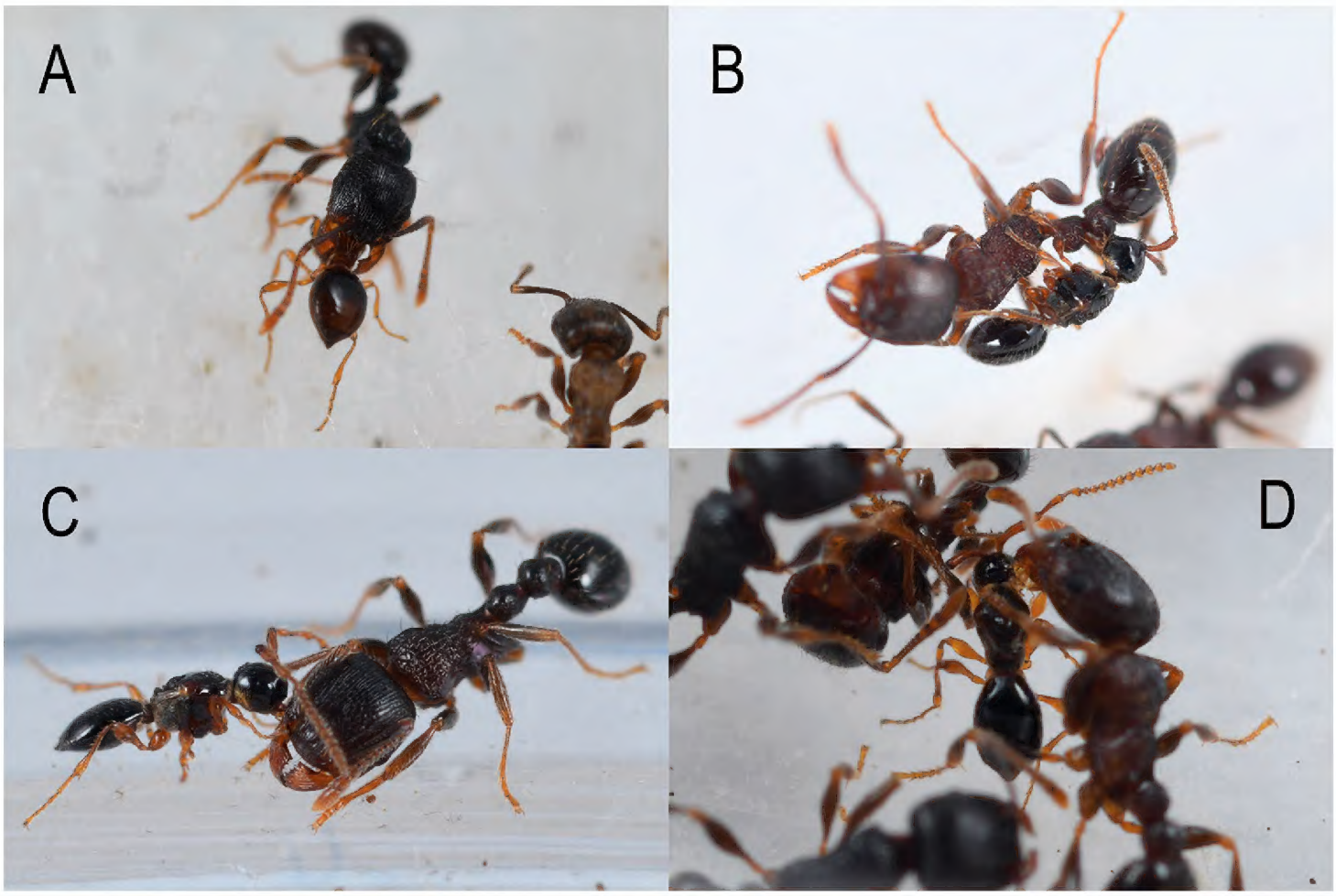

Figure 3. Interaction of *T. tortilis* and *Tetramorium tsushimae* (**A–D**): **A** worker ant biting petiole of female wasp **B** female wasp licking petiole of worker ant **C** male wasp licking head of worker ant **D** worker ant licking pronotum of male wasp.

characteristics of other species of the genus *Tetramopria* and the circumstances of the collection site, Kawai et al. (2024) considered these wasps were considered to have been associated with *Tetramorium tsushimae*. Specimens of *Tetramopria* sp. collected from *Tetramorium tsushimae* nests reported by Maruyama et al. (2013) were re-examined by RK and are also *T. tortilis*. Unfortunately, there are some errors in the collection dates and number of male and female specimens collected by Dr. T. Komatsu mentioned Maruyama et al. (2013), and we have provided the correct data above. So, Maruyama et al. (2013) was the first report of the biology of this species from Japan. During the current study SY collected adults of *T. tortilis* from nests of *Tetramorium tsushimae* during 2024, at Ulsan city (South Korea). The parasitoid host of *T. tortilis* is unknown but is probably a dipteran.

Behaviour. Courtship and copulation was observed by SY as follows: the male mounts the female with the two individuals facing the same way; the male grips the base of the females wings using the tibiae and tarsi of his mid leg and extends his forelegs laterally and hind legs posteriorly (Fig. 2A); the female may prevent further courtship by walking off in which case her antennae are held forward where they cannot be antennated (See Suppl. material 1); if the female is receptive, she will stand still and raise her antennae so that the male can antennate them (like Fig. 2A); the male strokes the female antenna alternately with each of his antennae bringing the RSS on his F2 into contact with the female antenna; if the male is not acceptable, she may try to push him away with her hind legs while the male uses his front and middle legs to

grasp and hold the female's mesosoma (Fig. 2B); if the female accepts the male, the male moves backwards, and copulation follows; probably the female signals her acceptance by bending both antennae backwards; the male inserts his genitalia into the female genital pore while grasping the female's metasoma with the fore and middle legs; during copulation the male's hind legs remain in contact with the substrate (Fig. 2C). Various interactions with host ants were observed by SY as follows: mouth to mouth contact between male or female wasp and worker ant (Fig. 2D, E); antenna and petiole biting of female wasp and carrying female wasp by ants (Figs 2F, 3A); pronotum licking of male wasp by ants (Fig. 3D); petiole licking of ants by female wasp (Fig. 3B); and licking of ant heads by male wasp were observed (Fig. 3C).

Tetramopria turbinata Notton, 1994

Figs 4, 5

Specimens examined. (1♂4♀♀) Japan • 1♂; Aichi Pref., Nisshin, Komenogi; MT; 25 VI–1 VII 2011; H. Seo leg.; (NBC) • 1♀; Mie Pref., Yokkaichi, Komatsu; YPT; 18–25 VI 1996; S. Hanaoka leg.; (NBC). South Korea • 3♀♀; Ulsan Metropolitan City, Ulju-gun, Cheongnyang-eup, Munjuk-ri; 24 VI 2024; Seonwoo Yoon leg.; from nest of *Tetramorium tsushimae*; (ELKU).

Diagnosis. Frons more convex than for *T. aurocincta*; female flagellum 10-segmented with 4-segmented gradually expanded clava; male F1 about 2.5 times as long as its greatest width. Propleuron smooth, with sparse short setae latero-ventrally (Fig. 4G). Anterior scutellar pit more or less costate (Fig. 4B, D); scutellar disc tectiform, with a sharp medial keel covering its entire length and extending forwards into anterior scutellar pit (Fig. 4B); scutellar disc emarginate posteriorly. Mesopleuron with scattered hairs in lower half, without pronounced ventral concavity in front of mid coxae. Male mid-trochanter and mid-tibia unmodified. Dorsal part of propodeum deeply foveate posteriorly (Fig. 4D, white arrow). T2 with two shallow subbasal foveae, very finely striate inside (Fig. 4D, green arrow).

Description. Female. Body length except ovipositor 2.3–2.8 mm. Body black and dark brown, except mandibles, antennae, tegulae and legs brown, scape and antennal club darker. Occipital, metapleural and pronotal pubescence golden, petiolar pubescence white.

Head. Head with short, semidecumbent to adpressed setae. Head in dorsal view as long as wide, hexagonal, tapered behind eyes. Head in lateral view slightly longer than high (17: 15), face slightly convex. Occiput with a dense cushion of setae. OOL: POL: LOL = 11: 5: 3. Eye small, its maximum width slightly longer than malar space (23: 21). Pleurostomal distance 0.6 times as long as maximum width of head. Basal margin of mandible costate. Mandible apically bidentate, only overlapping a little. Upper tooth of mandible shorter than lower tooth. Antenna with setae on all segments. Scape compressed, slightly curved, with reticulate-coriaceous sculpture (Fig. 4F). Pedicel longer than wide (16: 11). F1–F6 gradually widened towards apex. Flagellum with 4-seg-

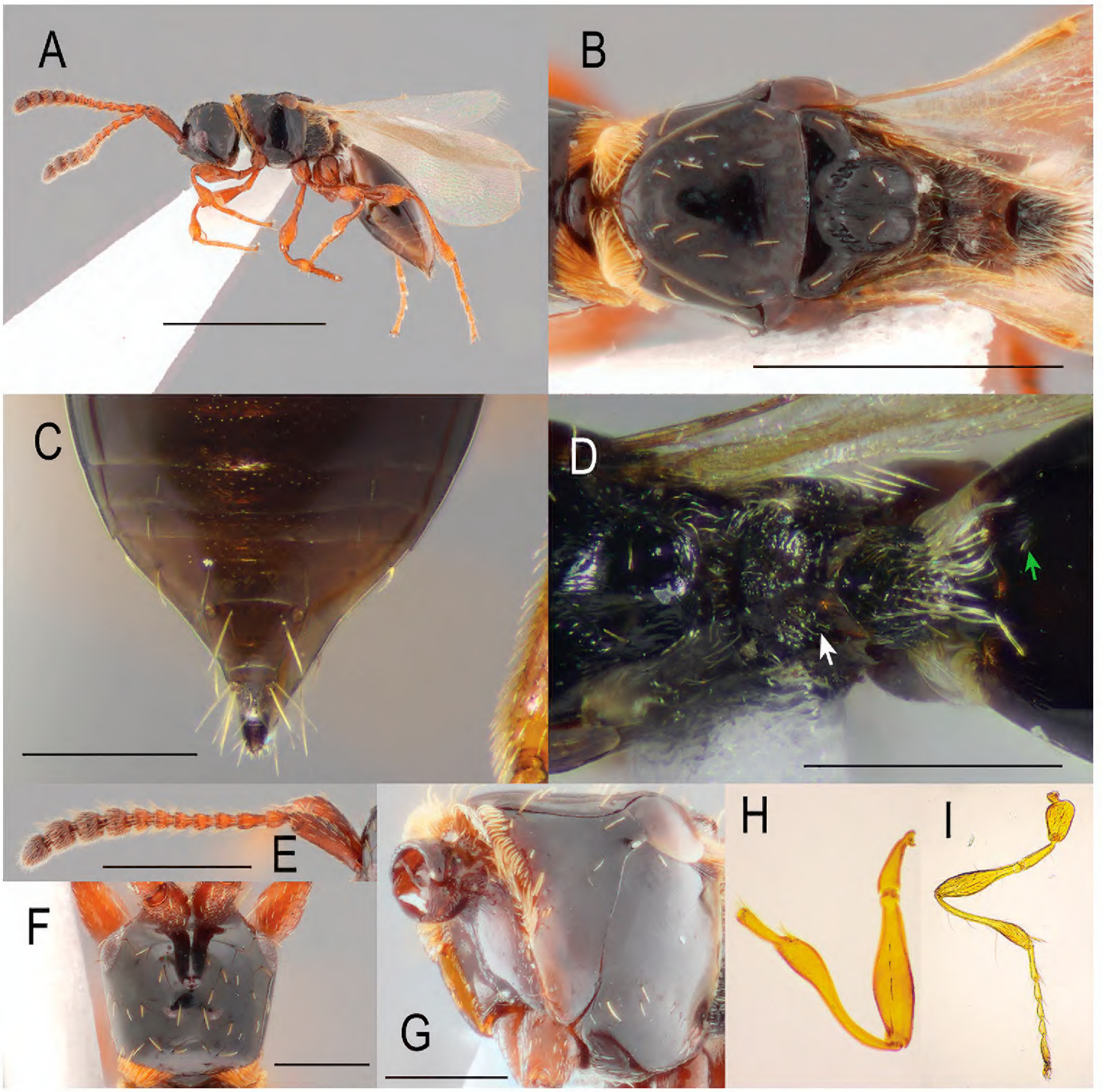

Figure 4. *Tetramopria turbinata* male from Japan (**H**), female from South Korea (**A–G**) and *Trichopria drosophilae* male from Japan (**I**): **A** lateral habitus **B** mesosoma, dorsal view **C** tip of metasoma, dorsal view **D** propodeum, petiole and anterior part of T2, dorsal view **E** antenna, lateral view **F** head, dorsal view **G** mesosoma, latero-ventral view **H** trochanter, femur, tibia and basitarsus of mid leg **I** mid leg; *white arrow* fovea of propodeum; *green arrow* fovea of anterior part of T2. Scale bars: 1.0 mm (**A**); 0.5 mm (**B, E**); 0.3 mm (**D**); 0.2 mm (**C, F, G**).

mented antennal club, its ventral part with dense sensilla. F10 conical. Ratios of length to maximum width of each flagellomeres in lateral view: F1 19: 10; F2 15: 10; F3 13: 10; F4 12: 11; F5 12: 13; F6 12: 14; F7 16: 18; F8 19: 20; F9 19: 20; F10 22: 16.

Mesosoma. Mesosoma slightly wider than head (39: 35). Pronotal collar wide, vertical, with a dense cushion of setae, interrupted at top of pronotum (Fig. 4B). Pronotal shoulder rounded. Lateral part of pronotum smooth and shiny. Propleuron smooth, with sparsely short setae latero-ventrally (Fig. 4G). Mesoscutum smooth, convex anteriorly,

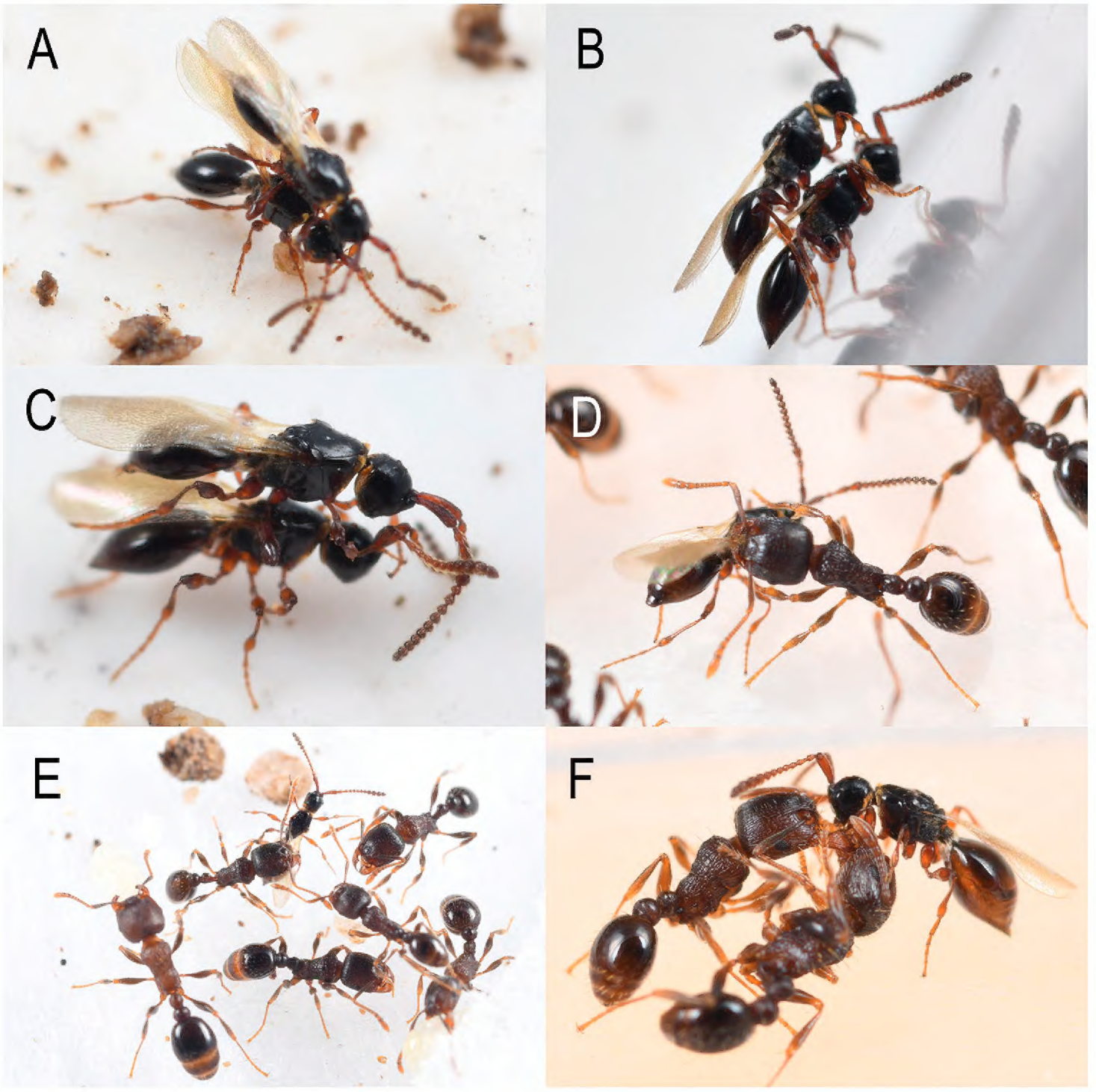

Figure 5. Courtship of *Tetramopria turbinata* (**A–C**) and interaction of *T. turbinata* and *Tetramorium tsushimae* (**D–F**): **A, B** mounting – male wasp holding the female's wings with his mid legs **C** antennation – male wasp with his F2 in contact with the female antennal clava, also the male wasp is holding the female's scapes with his front tarsi **D** worker ant biting base of fore wing of a male wasp **E** worker ant biting base of fore wing of a female wasp **F** mouth to mouth contact between a female wasp and a worker ant.

flat posteriorly with 5–10 short semidecumbent setae. Anterior scutellar pit transverse, curved, costate, divided into small foveae (Fig. 4B, D). Scutellar disc weakly convex, sulcate laterally and posteriorly. Medial keel of scutellar disc covering its entire length and extending forwards into anterior scutellar pit. Mesopleuron smooth, without median oblique impression and few scattered setae. Mesopleuron in lateral view convex posteroventrally, in front of mid coxal insertion, not concave like *T. tortilis*. Metascutellum with strong median keel and lower lateral keel. Metapleuron with short, adpressed setae laterally, and long setae dorsally (Fig. 4A). Lateral part of propodeum with short, adpressed

setae anteriorly, with a band of long setae behind that, and the posterior margin of the propodeum bare. Dorsal area of propodeum with adpressed setae. Medial keel of propodeum simple, strongly developed, raised anteriorly. Propodeum with lateral keel developed, posteriorly produced as a tooth. Posterior margin of propodeum concave. Basal part of all femora compressed and reticulate-coriaceous. Apical part of all femora enlarged and smooth. Basal part of mid and hind tarsi laterally compressed, smooth and shiny.

Metasoma. Petiole in lateral view slightly raised, dorsally visible part 1.1 times as long as its maximum width, covered with short adpressed setae anteriorly and longer setae posteriorly. Metasoma in dorsal view about 1.8 times as long as its maximum width, wider than mesosoma (95: 78). Postpetiole comprising six smooth, clearly differentiated tergites. T2–T5 with micropunctation medially (Fig. 4C). Anterior margin of T2 slightly concave with two shallow foveae, very finely striate inside. T3 and T4 with a pair of setae, T5 with three pair of setae, T6 with a pair of spiracles. T7 with pygostyles surrounded by several setae. Postpetiole comprising five smooth, shiny, clearly differentiated sternites. Anterior margin of S2 with two deep foveae covered with long setae. S3–S6 covered with micropunctation medially. Posterior part of S6 with several setae. Ovipositor sometimes slightly exposed.

Distribution. Japan (Honshu: Aichi, Mie), new record; South Korea (Notton 1994).

Biology. *Tetramopria turbinata* has been collected from the nests of *Tetramorium tsushimae* in South Korea by SW. In Japan, associated ants are unknown. The parasitoid host of *T. turbinata* is unknown but is probably a dipteran.

Behaviour. Courtship was observed by SY as follows: the male mounts the female with the two individuals facing the same way; the male grips the base of the females wings using the tibiae and tarsi of his mid leg (Fig. 5A), grips the female face or scapes with his fore tarsi (Fig. 5A, B), and extends his hind legs posteriorly or places them on the female metasoma; if the female is receptive, she will stand still and raise her antennae a little so that the male can antennate them; the male strokes the female antennae alternately with each of his antennae bringing the RSS on his F2 into contact with the female antenna (Fig. 5C). Successful courtship and copulation was not observed. Various interactions with ants were observed by SY as follows; mouth to mouth contact between female parasitoid and worker (Fig. 5F), biting of the base of the fore wing of male or female parasitoid by ants (Fig. 5D, E).

Discussion

Many diapriid wasps have morphological characteristics and/or collection records suggesting an association with ants which allow us to infer that they are more or less adapted as myrmecophiles. In the subfamily Belytinae, for example, there are records of species collected from ant nests, such as *Acanosema rufum* Kieffer, 1908, *Synacra brachialis* (Nees, 1834) and *S. sociabilis* (Kieffer, 1904) (Nixon 1931, 1957; Huggert 1979; Macek 1995; Kawai 2023). On the other hand, many species of the subfamily Diapriinae, including *Tetramopria* are known to have morphological characteristics

(reduced eye size; reduced pigmentation; additional setation and dealation by the host ants) that suggest a more intimate relationship with ants, especially in the New World (Huggert and Masner 1983; Loiácono 1981, 1987, 2000; Loiácono et al. 2000; Loiácono and Margaría 2002). Behavioural interactions of many species known as parasites or parasitoids with host ants are still poorly understood (Hölldobler and Kwapich 2022), however the current study allows us to make some novel observations of interactions between these two *Tetramopria* species and their host ants which confirm that they are in fact well adapted myrmecophiles:

a. Mouth to mouth contact with host ants was observed for both *Tetramopria* species. In the Diapriinae, such behaviour has been observed previously in *Solenopsia imitatrix* and *Lepidopria pedestris* by Hölldobler (1928), Lachaud (1980) and Lachaud and Passera (1982). This is the first observation of trophallaxis in the genus *Tetramopria*. Similar trophallaxis has also been observed for some non-diapriid myrmecophilous Braconidae, e.g. *Paralipsis enervis* (Nees, 1834) and *Paralipsis eikoae* (Yasumatsu, 1951) (Starý 1966; Takada and Hashimoto 1985).
b. Host ants were observed to lick wasps of *Tetramopria tortilis*. This behaviour has previously been observed for example in *Tetramopria aurocincta* which is licked by its *Tetramorium caespitum* host ants (Wasmann 1909). The significance of this behaviour requires further explanation, it may simply be grooming, or possibly the wasps actively secrete substances that are attractive to ants and modify the ant's behaviour.
c. Host ants were seen to bite the base of wings of *Tetramopria turbinata*. This behaviour may be connected with the phenomenon of secondary apterism or dealation which has been reported in numerous taxa of myrmecophile Diapriinae (e.g. Loiácono et al. 2002; Masner and García 2002). This is the first time that wing biting behaviour by ants has been directly observed in Diapriidae. In one experiment a wasp with fully-developed wings was placed in the observation ant nest, its wings were bitten off after about 10 days. Similar behaviour has also been observed for the ant hosts of some non-diapriid myrmecophilous Braconidae e.g. *Paralipsis enervis* (Nees, 1834) (Starý 1966) and Chrysididae e.g. *Rhadinoscelidia lixa* Hisasue & Mita, 2020 (Hisasue and Mita 2020).
d. Host ants were seen to bite the antennae and petiole of *Tetramopria tortilis*, and carrying the wasps about. This behaviour has previously been observed for example in *Solenopsia imitatrix* by Hölldobler (1928) who noted the wasp was once carried around in the nest for a long time by the petiole, with its back turned to the carrier. It is not entirely clear if this is an aggressive response or whether the ants are simply moving the wasps as they would move their brood. More observations are needed to clarify this point.

The novel observations of the courtship behaviour of both *Tetramopria* species presented above allow some intriguing comparisons with other Diapriini from

which they show some significant differences in behaviour and associated morphology. The account of the mating behaviour of *Trichopria sociabilis* Masner, 1965 by Postu et al. (2013) provides a useful comparison as this species is probably the species most closely related to *Tetramopria* for which mating has been observed. Other informative observations were made by Romani et al. (2008) and Liu et al. (2017) on the mating of *Trichopria drosophilae* (Perkins, 1910). Here are some of the special features we noticed:

a. Both males of *Tetramopria tortilis* and *T. turbinata* grip the base of the female's wing with their mid legs, whereas Postu et al. (2013) report that *Trichopria sociabilis* grips the propodeum of the female instead.
b. In particular the male of *Tetramopria tortilis* adopts an unusual position when mounted, holding on with only the mid legs, the fore and hind legs being extended. This appears to be a consequence of modifications of the mid leg, notably the expanded trochanter, perhaps housing additional muscle, and modifications of the tibia and basitarsus, interpreted here as structures for enhancing grip. In contrast *T. turbinata* does not rely only on the mid legs to grip the female when mounted, the position of the fore and hind legs are similar to that of *Trichopria sociabilis* reported by Postu et al. (2013).
c. Both males of *Tetramopria tortilis* and *T. turbinata* when mounted are able to antennate when the female antennae are more extended anteriorly. This appears to be a consequence of the male basal antennal segments, especially F1-2, being more elongate, whereas the female antennae are held erect during antennation for *Trichopria sociabilis* as reported by Postu et al. (2013) and also for *T. drosophilae* according to Romani et al. (2008).
d. Females of *Tetramopria tortilis* appear to show readiness for copulation by moving both antennae backwards, this appears to be shared with *Trichopria drosophilae* as reported by Romani et al. (2008), probably this is present for *T. sociabilis* but was missed by Postu et al. (2013) since they did not consider female acceptance behaviour.
e. *Tetramopria* species appear to be similar to *Trichopria sociabilis* in lacking any wing fanning before mating (Postu et al. 2013), whereas, for *Trichopria drosophilae* the male fans his wings before attempting to mount (Romani et al. 2008).

It is too early to provide a detailed overview of mating behaviour of Diapriini however it is now clear that there is significant variation within the tribe which merits further study: some of the features of courtship of *Tetramopria* may be connected to their myrmecophile habits, for example the ability of males to antennate the female antenna in a more extended position may be advantageous in confined spaces, also the specialised and likely more powerful mid leg grip may be helpful in the hustle and bustle of the ant nest.

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Supplementary material 1

Supplementary movie

Authors: Seonwoo Yoon

Data type: mov

Explanation note: The female of *Tetramopria tortilis* may prevent further courtship by walking off.

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